

## GROUPING PATTERNS IN A FOREST DWELLING POPULATION OF PYRENEAN CHAMOIS

J. HERRERO<sup>1</sup>, I. GARÍN<sup>2</sup>, A. GARCÍA-SERRANO<sup>3</sup>,  
R. GARCÍA-GONZÁLEZ<sup>4</sup> & A. ALDEZABAL<sup>5</sup>

<sup>1</sup> Ecology Department, Faculty of Biology, University of Alcalá. E-28871 Alcalá de Henares.  
E-mail: egasl@arrakis.es

<sup>2</sup> Zoology and Animal Cell Dynamics Department, University of the Basque Country. P. O. Box 644.  
E-48080. Bilbo. E-mail: zopgaati@lg.ehu.es

<sup>3</sup> Ega Wildlife Consultants, Sierra de Vicort, 31. 1º A. E-50003. Zaragoza

<sup>4</sup> Pyrenean Institute for Ecology, CSIC. P. O. Box 64. E-22700. Jaca. E-mail: rgarcia@ipe.csic.es

<sup>5</sup> Ecology and Plant Ecology Department, University of the Basque Country. P. O. Box 644. E-48080. Bilbo.  
E-mail: gopalron@lg.ehu.es

**ABSTRACT.**— Diurnal grouping in a population of Pyrenean chamois *Rupicapra p. pyrenaica* was studied by direct observation on the edge of their westernmost distribution. The whole area occupied by a population was surveyed by performing monthly fixed transects over one year. The size of 214 groups ranged from 1 to 54. Both size and composition were quite variable and differed between seasons and habitats. Groups were generally very small (45% of only one animal, median: 2;  $P_{75}=4$ ), which is characteristic of small and low density forest-dwelling populations. Groups appeared to depend strongly on the annual biological cycle, food distribution and vegetation cover. The spatial segregation between males and females was only evident in the summer, when solitary males mostly occupied the forest and females with kids lived on open pastureslands. All the general patterns on size and composition of the groups occurred in this population.

**RÉSUMÉ.**— Par la voie de l'observation directe nous avons étudié le gréganisme journalier chez une population d'isard (*Rupicapra p. pyrenaica*) à la limite occidentale de l'aire de répartition de l'espèce. La surface complète occupée a été suivie par de trajets fixes mensuels durant un an. La taille des différents troupeaux a varié de 1 à 54 individus. De même, la composition était également très variable et changeait d'une saison à l'autre ou d'un habitat à l'autre. De manière générale, les troupeaux étaient très petits (45% de seulement un animal, moyenne : 2 ;  $P_{75}=5$ ), c'est la caractéristique des petites populations, à basse densité et vivant en forêt. Les groupes étaient fortement conditionnés par le cycle annuel, la distribution des ressources alimentaires et le recouvrement végétal. La ségrégation spatiale entre mâles et femelles avait lieu seulement en été, moment où les mâles solitaires occupaient surtout la

forêt tandis que les femelles avec les petits préféraient les pâturages ouverts. Concernant la taille et la composition des troupeaux, tous les patrons généraux ont été mis en évidence sur cette population.

**RESUMEN.**– Se estudió por observación directa el gregarismo diurno en una población de sarrío *Rupicapra p. pyrenaica* en el límite occidental de distribución de la subespecie. La totalidad del área ocupada fue objeto de seguimiento a partir de recorridos fijos mensuales durante un año. El tamaño de 214 grupos fue de 1 a 54 individuos. Tamaño y composición fueron muy variables y diferían entre estaciones y hábitats. Los grupos eran generalmente muy pequeños (45% de solamente un animal, mediana: 2;  $P_{75}=4$ ), lo que es característico de poblaciones pequeñas, de baja densidad y hábitat boscoso. Los grupos dependían fuertemente del ciclo anual, distribución del alimento y cobertura vegetal. La segregación espacial entre machos y hembras ocurría solamente en verano, cuando los machos solitarios ocupaban principalmente el bosque y las hembras con crías vivían en pastos abiertos. Todos los patrones generales referentes a tamaño y composición de los grupos, se observaron en la población.

**Key-words:** *Rupicapra pyrenaica pyrenaica*, Pyrenees, group size and composition, seasonal and habitat variation, biological cycle.

## 1. Introduction

The genus *Rupicapra* is today considered divided into two species: *R. pyrenaica*, living naturally in the Pyrenees, Cantabrian Mountains and Abruzzo; and *R. rupicapra*, in the Alps, Tatra Mountains, Anatolia, the Caucasus and several European massifs (NASCETTI *et al.*, 1985).

The Pyrenean chamois *Rupicapra pyrenaica pyrenaica* (CABRERA, 1914; NASCETTI *et al.*, 1985), is a gregarious, lowly dimorphic, cliff-dwelling mountain ungulate living exclusively in the Pyrenees mountain chain and totalling today about 40,000 animals (HIDALGO *et al.*, 1995).

Recently, the interest for this important primary consumer in Apennines, Alps and Pyrenees and the possibilities for its ethological study as it is easily sightable, has allowed to undertake several studies on the genus, considering different aspects of its biology (ELSNER-SCHACK, 1985; RICHARD-HANSEN *et al.*, 1992). One of the subjects that has driven more attention has been social structure or grouping (RICHARD-HANSEN, 1992; BON *et al.*, 1992,) *i. e.* the spatial and temporal interaction of the different age and sex classes of a population. This is a characteristic of many ungulate species, which aggregate or disperse as a result of environmental and ethological factors, which show variable group size and composition in response to environmental and ethological factors.

The kind of group in each particular moment is due to satisfy individual requirements, the kind of aggregation being optimal under a given circum-

stance, even if to a certain extent chance can be important. The size and composition of the groups respond to a variety of factors (GEIST, 1974), as different as habitat (ALADOS, 1985; ELSNER SCHACK, 1985); food (SCHALLER, 1977; BERDUCOU, 1974); population density; sexual behaviour; differential "sociability" of sexes and ages (RICHARD-HANSEN, 1992); antipredatory behaviour (GEIST, 1974; SCHALLER, 1977), etc. As a result, ungulates normally show a great variability in their grouping patterns, even inside the same species (RICHARD-HANSEN, 1992; MAUBLANC *et al.*, 1987; EDGE & OLSON, 1990). Chamois show a plastic social structure, in relation with sex, density and seasons. The research on this subject allows to understand the influence of the factors affecting group's size and composition. In spite of this great variability, the main relationship is mother-kid and can go on until the second year of the kid's life (RICHARD-HANSEN, 1992). The greater seasonal variations are shown by male sociability, which can be solitary, live in male groups (BERDUCOU & BOUSSES, 1985) or in mixed groups (only subadult males in the case of Appennine chamois, (LOVARI & COSENTINO, 1986).

This flexibility makes grouping a reflection of biological and environmental factors, and allows researchers and managers to use it as an indicator of the population status in a given environment. It is also easy and quick to use, which makes it attractive for management and long-term monitoring.

The aim of this work is to describe the diurnal social strategy of a population of Pyrenean chamois during one annual cycle, living in a predominantly forested habitat and representing the westernmost range area of the subspecies.

## 2. Material and methods

The study was conducted in Larra-Belagoa Nature Reserve, a protected area of 57400 ha, in a rugged karstic relief the southwestern Pyrenees (Region of Navarre, Spain). The altitude ranges from 1100 to 2442 m a. s. l., annual precipitation reaches 2000 mm per year, and the annual mean temperature at 1500 m a. s. l. is 7°C. During our field work there was particularly low snow precipitation.

The Pyrenean chamois is not hunted in this area and is considered "Vulnerable" in the Navarrian Regional List of Endangered Species. Demographic population characteristics are as follows: a total count of about 110 animals with a density of 5.2 km<sup>-2</sup> and a sex-ratio of 0.63 males per female (GARIN & HERRERO, 1997). In its westernmost distribution limit the subspecies is limited to the Natural Reserve. Other wild ungulates present are wild boars *Sus scrofa* and roe deer *Capreolus capreolus*. Sheep, cattle and horses are present from June to October in the supraforestal pastures, above timber-

line. A small group of less than 50 domestic goats were found there all year long. The Reserve has a low human frequentation, at least considering the Chamois range, so animals are not habituated to the human presence.

From February 1992 to January 1993 at least four monthly surveys were undertaken. The surveys were done on foot, on skis and snowshoes during the period of snow, which lasted 5.5 months, and were carried out from sunrise to mid afternoon. When heavy snow was present, the surveys did not reach the higher altitudes, but observations were made from fixed points. We assumed that the surveys were representative of available habitats and altitude range in the study area in each month of the year.

We have used SCHALLER's (1977) definition in which a group is an aggregation of individuals occupying the same patch of habitat, with sensorial contact between them, and more or less coordinated in their movements. We consider also as a group one solitary animal.

Group recording was done with the scan-sampling method (ALTMANN, 1974), using 8 x 30 binoculars, spotting scopes (20-60) and altimeters.

Although the survey was carried out monthly, we grouped the data into bimonthly periods to increase the statistical power of the tests due to the small monthly samples. Dividing the year into bimonthly periods yields more natural units which are easily related to the Chamois annual cycle, and have already been used by other authors for the species (ELSNER SCHACK, 1985). The two-month periods were: Early Winter (January and February), Late Winter (March and April), Births (May and June), Summer (July and August), Autumn (September and October) and Rut (November and December).

Chamois were classified by age and sex considering their morphological characteristics: adult males, adult females, yearlings and kids.

Habitat units were defined from a vegetation map (ELÓSEGUI *et al.*, 1986). The dominant types were: Mixed Beech *Fagus sylvatica* and Fir *Abies alba* Forest (Beech and Fir); Beech and Fir with Mountain pine *Pinus uncinata* (Beech and Pine); Mountain pine wood (Pine); Cliffs (Rocks) and Meadows (Pasture). The mountain pine habitat is a clear forest with rocks and a dense herbaceous layer.

To describe the social structure we considered size (number of animals in the group) and composition (sex and age) of the groups, habitat used and bimonthly period of the year. Every animal was considered as a unit (PUTMAN, 1986).

We used non-parametric tests due to the non normal distribution of data. Group's size variation was tested through the median test, recommended for highly asymmetrical distributions (CLUTTON BROCK *et al.*, 1982; ELSNER SCHACK, 1985; LOVARI & COSENTINO, 1986; FOX *et al.*, 1992; PÉREZ-BARBERÍA & NORES, 1994).

### 3. Results

A total of 214 groups were recorded, totalling 837 chamois. The most frequent group was one individual (45%). Sightings of large groups were scarce: only 4 groups were bigger than 20 animals (1.9%). The maximum group size was 54. Median group size was 2, and percentil 75 ( $P_{75}$ ) was 4 (Figure 1).

Group size differed considering habitats (Median test:  $\chi^2=8,58$ ;  $N=837$ ;  $p=0.035$ ) (Table 1). In the Beech and Fir forest, groups were smaller than in Pasture and Rocks, which represent the open habitats. In the Pine forest group size was more homogeneous than that in Rock and Pasture. Pasture showed also the biggest aggregations.

There was a significant difference between the size of the groups in bimonthly periods (Median test:  $\chi^2 90.2$ ;  $N=837$ ;  $p=0.009$ ). Births is the most variable season regarding group size (Table 2). This period shows the smaller and the larger groups.

Regarding group composition, only 142 groups were considered as the sex and age of all their animals were recorded. Of the 17 possible aggregation combinations of the four categories of sex and age, only 13 were found. We grouped them into six new ones: lonely males; all-male groups; mixed group [females with kids, males (mostly 1) and eventually yearlings]; matriarcal

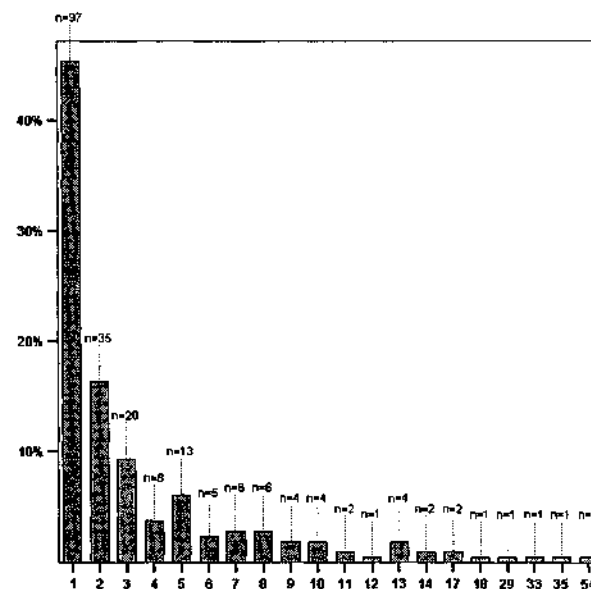


Figure 1. Grouping patterns of Pyrenean chamois in Larra-Belagoa Natural Reserve.

group (females with kids and eventually yearlings); solitary females and yearling groups (of one or more yearlings) (Table 3).

Populations' group composition varied along the year. All-male groups are scarce and small, with generally only 2 males. Solitary males groups appeared all year long, specially during rut, and were minimal at the end of the winter. Lonely females are less frequent than lonely males. Lonely females appear specially during births period. Matriarcial and mixed groups total 50% of the groups, and have similar proportion of occurrence. Matriarcial groups

Table 1. Group size in relation to habitat by Pyrenean chamois in Larra-Belagoa Natural Reservation.

HABITATS	GROUPS	MEDIAN	MODE	AVERAGE	MAXIMUM	$P_{75}$	TOTAL
BEECH	3	1	1	1,3	2	2	4
BEECH AND PINE	22	1	1	1,9	8	3	43
PINE	98	2	1	3,4	35	3	336
PASTURE	69	3	1	5,2	54	7	357
ROCKS	22	2	1	4,4	14	7	97
TOTAL	214	2	1	3.9	54	4	837

$P_{75}$ : percentil 75.

Table 2. Seasonal group size by Pyrenean chamois in Larra-Belagoa Natural Reservation.

PERIODS	GROUPS	MEDIAN	MODE	AVERAGE	MAXIMUM	$P_{75}$	TOTAL
EARLY WINTER	29	2	1	4.14	18	5	120
LATE WINTER	14	3	3	3.21	8	4	45
BIRTHS	37	1	1	4.54	54	1	168
SUMMER	42	2	1	3.81	17	5	160
AUTUMN	52	2.5	1	4.29	35	5	223
RUT	40	2	1	3.03	10	4	121
TOTAL	214	2	1	4	54	4	837

$P_{75}$ : percentil 75.

Table 3. Seasonal group structure by Pyrenean chamois in Larra-Belagoa Natural Reservation.

GROUPS	EARLY	LATE	BIRTHS	SUMMER	RUT	AUTUMN	TOTAL (%)
	WINTER (N=21)	WINTER (N=8)					
SOLITARY MALES	7	1	6	5	12	8	39 (28%)
ALL MALE	1	0	0	1	1	3	6 (4%)
MIXED	5	5	4	2	7	11	34 (24%)
MATRIARCAL	4	2	2	13	4	12	37 (26%)
SOLITARY FEMALES	3	0	9	5	2	1	20 (14%)
YEARLINGS	1	0	4	1	0	0	6 (4%)
TOTAL	21	8	25	27	26	32	139

N: number of groups.

are more common during summer and less frequent during the rut. Mixed groups occur all year long, with a minimum during summer and a maximum at the end of winter. Mixed and matriarcal groups have an inverse, being mixed groups minimal and matriarcal maximal in summer. Lonely or yearling groups are also scarce and appear frequently in matriarcal or mixed groups. Yearling groups are more frequent during the births period.

#### 4. Discussion

Larra-Belagoa's Pyrenean chamois social structure changes throughout the year as response to the variations in resource and food availability and reproductive cycle. Due to the small sample and low population density the most unfrequent aggregations do not happen. There are no stable groups but a general trend of each sex and age which to associate with itself (RICHARD-HANSEN, 1992). There is also a great sociability of all the sex and age classes as most of the possible aggregations were found.

Open habitats favour big groups and forest small ones. This seems to be the rule for different ungulate species (GERARD *et al.*, 1992). Forests and rough relief, favour small groups as sight contact between individuals is more difficult at great distance, while open environments help to form large ones (CLUTTON-BROCK *et al.*, 1982).

Food supply is also an important factor. When it is concentrated produces an attraction on individuals and consequently promotes the formation of large groups (ELSNER-SHACK, 1985). If it is dispersed as happens in winter, groups should be small (BERDUCOU, 1974). Theoretically, considering what happens in other populations, food in winter is scarce and scattered and consequently groups are small (BERDUCOU, 1974), because small groups diminish food competition (MAUBLANC *et al.*, 1987). Nevertheless, in spring and autumn, food availability is higher and groups bigger. During summer big aggregations occur, because of the Chamois concentration in preferred feeding areas (GARCÍA-GONZÁLEZ *et al.*, 1985).

Antipredatory behaviour in open environments should favour large groups, as this increases individual efficiency. Even sex-ratio and productivity are demographic aspects that may determine social patterns (RICHARD-HANSEN *et al.*, 1992) which in turn are affected by density. Finally, density is one of the most important social factors. High density promotes large groups, male groups and large matriarcal groups (BERDUCOU & BOUSSES, 1985; GERARD *et al.*, 1995; PÉREZ-BARBERÍA & NORES, 1994), though this was argued by LOVARI & COSENTINO (1986). This should diminish spatial segregation between sexes and ages and consequently their competition (COUTURIER, 1962).

In Larra-Belagoa, large groups appear from May to September and the larger ones in summer (RICHARD & MENAUT, 1989). There is a relative homogeneous small group size all year round except in the Births period, which exhibit the smaller and bigger groups (RICHARD & CAMPAN, 1992). This is because females split before parturition (GONZALEZ & BERDUCOU, 1985) and aggregate afterwards, making kindergartens with the new born kids. It is probably an antipredator behaviour in the period in which young are more vulnerable, where kid care is optimized, diminishing also the time spent in vigilance and increasing feeding activity (PÉPIN & LAMERENX, 1995). We must notice that the population showed a different annual habitat use compared with the general pattern, with a less marked seasonal migration and a mainly forest use all year long (HERRERO *et al.*, 1996) which determines the existence of smaller groups.

Mixed groups occur all year round, and not only during rut. Males show a keeping behaviour with respect to females that goes much further than a simple spatio-temporal coincidence. In the Appennines, mixed groups represent two thirds of the total groups (LOVARI & COSENTINO, 1986). A possible justification of mixed groups abundance during all the year is low density. In the Alpine ibex *Capra ibex*, COUTURIER (1962) found the same situation. NIEVERGELT (1974) relates this situation with habitat in the Ibex and in the Walia ibex *Capra waliae*. In other partial surveys carried out in the Pyrenees its absence or scarcity during summer had led to believe that this was the general pattern outside the rut (GARCÍA-GONZÁLEZ, 1985; GARCÍA-GONZÁLEZ *et al.*, 1987).

The low male sociability may be the reason for which they are more solitary. Solitary males are more common than lonely female ones and male groups are scarce. Due to the high density in the near French Pyrenees National Park, male groups are common and concentrate up to 64 (GONZALEZ & BERDUCOU, 1985). In this case males are predominantly solitary or in all-male groups as in other populations (RICHARD & MENAUT, 1989; GONZALEZ & BERDUCOU, 1985) and at the same time form small groups (LOVARI & COSENTINO, 1986). The low frequency of male groups could also be explained by low density (BERDUCOU & BOUSSES, 1985) as in low density areas they are normally rare and small (RICHARD & MENAUT, 1989), even though other authors disagree pointing out other possible reasons (LOVARI & COSENTINO, 1986). LEVET & PÉPIN (1994) concluded that sociality was higher in young males in a very high density population (over 30 Pyrenean chamois km<sup>-2</sup>).

The male social seasonal variability is responsible for the variation in the proportion of male, mixed and matriarcal groups. The higher frequency of lonely males and all-male groups is during rut. In the Appennines the all-



male groups appear only during rut and are normally young animals. The reason could be an exclusive participation of old males in the formation and care of harems (LOVARI & COSENTINO, 1986). This could be the pattern in our study area, a non-hunted and 'longeve' population with old males participating in reproduction and young that are kept apart meeting in all-male groups. In the Cantabrian chamois *Rupicapra pyrenaica parva* no all-male groups were found during rut in a hunting reservation, probably because only the supraforestal portion of the population was being surveyed (PÉREZ-BARBERÍA & NORES, 1995). Another possibility is that all the males were participating in the reproduction since the population was hunted probably sex-ratio should be balanced towards females.

Males show a summer spatial and social segregation (in the sense of BON *et al.*, 1992) as in other Chamois populations (Alpine chamois, SHANK, 1985; Apennine chamois, LOVARI & COSENTINO, 1986; Pyrenean chamois, GERARD & RICHARD-HANSEN, 1992; GARCÍA-GONZÁLEZ & HIDALGO, 1989; Cantabrian chamois, PÉREZ-BARBERÍA & NORES, 1994) though there is not a marked social segregation during the rest of the year, compared with other populations. This pattern means that there is an antagonic variation in the proportion of mixed and matriarcal groups, suggesting a spatial segregation of males and females with kids when food availability is a higher. This situation can favour males (SHANK, 1985) or lactating females (ESCÓS & ALADOS, 1992), to occupy the best feeding areas. Other authors find an altitudinal segregation also in winter (LOVARI & COSENTINO, 1986). In the particular case of Larra-Belagoa feeding areas can be considered of similar feeding quality as both the herb layer of the mountain pine forest and the open pastureland are rich and dense during summer. However the forest represents a safer habitat.

At the end of winter, male integration in female groups reaches its higher value and the male groups its lower. This minimal segregation is probably a response to food scarcity.

Yearling groups are rare. Their frequency is higher when yearling males are theoretically chased from mixed and matriarcal groups (GONZALEZ & BERDUCOU, 1985).

Harem size is small because of the low density and proportional sex-ratio. Open habitats with higher visibility represents better areas to keep harems for males which can control females and other opponent males more easily as happens in Red deer *Cervus elaphus* (CLUTTON-BROCK *et al.*, 1982).

The comparison of social structure between chamois populations is difficult. Most studies have not been carried on during a whole annual cycle or have not been undertaken also in the forest, which is used mainly in the snow period. Demographic parameters are also commonly lacking. They are

important to understand the social pattern in that particular population (GERARD & RICHARD HANSEN, 1992): absolute abundance, total census, density, fertility and sex-ratio. This allows to know the relative proportion of the age and sex classes, that exhibit different level of sociality.

Considering a predominantly forested habitat, low density, few animals, a high sex-ratio and the rough relief; we should expect to find small groups (GONZALEZ & BERDUCOU, 1985), small and highly frequent all-male groups and low spatial and social sex segregation (RICHARD-HANSEN, 1992). This general pattern has occurred. Some hypothesis on general patterns of social structure as the idea that small groups should appear in closed habitats and low density populations happen in Larra-Belagoa, though others do not, because female with kids, yearlings and males are frequent, and sex ratio does not lead to a high frequency of all-males groups (GERARD *et al.*, 1995), may be because other demographic features are missing in the model.

Finally, the coincidence between the theoretical and the real social structure pattern, depending on the environment and demographic parameters mean that grouping can be an important diagnosis of the social and population status. Its application in census and long time monitoring could be very useful.

**Acknowledgments.** We are grateful to D. Saavedra and all the others who helped in the field work. This paper is part of a research granted by the Regional Government of Navarre on Pyrenean chamois biology.

### References

- ALADOS, C. (1985). Group size and composition of the Spanish ibex (*Capra pyrenaica* Schinz) in the Sierras of Cazorla and Segura. In LOVARI, S. (Ed.). *The biology and management of mountain ungulates*: 134-147. Croom Helm, London.
- ALTMANN, J. (1974). Observational study of behaviour: sampling methods. *Behaviour*, 49: 227-267.
- BERDUCOU, C. (1974). *Contribution à l'étude d'un problème éco-physiologique pyrénéen: l'alimentation hivernale de l'isard*. Ph. D. thesis, University of Toulouse, Toulouse.
- BERDUCOU, C. & BOUSSES, P. (1985). Social grouping of a dense population of chamois in the Western Pyrenees National Park. In LOVARI, S. (Ed.). *The*

- biology and management of mountain ungulates*: 166-175. Croom Helm, London.
- BON, R.; GONZÁLEZ, G.; BOSCH, M. L. & CUGNASSE, J. M. (1992). Ram rut-involvement in a hunted population of mouflons. *Acta Theriologica*, 37: 63-71.
- CABRERA, A. (1914). *Fauna Ibérica. Mamíferos*. Museo Nacional de Ciencias Naturales. 441 pp. (In Spanish).
- CLUTTON-BROCK, T. H.; GUINNES, F. E. & ALBONS, S. D. (1982). *Red deer. Behavior and Ecology of Two Sexes*. Univ. Press. Edinburgh, Scotland, United Kingdom.
- COUTURIER, A. J. (1962). *Le bouquetin des Alpes (Capra aegargus ibex ibex L.)*. Published by the author, Grenoble.
- EDGE, W. D. & OLSON-EDGE, S. L. (1990). Poulation characteristics and group composition of *Capra aegargus* in Khirtar National Park, Pakistan. *J. Mammal.*, 71 (2): 156-160.
- ELÓSEGUI, J.; SANTESTEBAN, I. & SOLÉ, J. (1986). El Parque Natural pirenaico en Navarra. I. Larra-Belagoa. Gobierno de Navarra. Pamplona.
- ELSNER-SCHACK, I. VON. (1985). Seasonal changes in the size of chamois groups in the Ammergau mountains, Bavaria. In LOVARI, S. (Ed.). *The Biology and Management of mountain Ungulates*: 148-153. Croom Helm, London.
- ESCÓS J. & ALADOS, C. L. (1992). Habitat preference of Spanish ibex and other ungulates in Sierras of Cazorla and Segura. *Mammalia*, 56 (3): 393-406.
- FOX J. L.; SINHA, S. P. & CHUNDAWAT, R. S. (1992). Activity patterns and habitat use of ibex in the Himalaya Mountains of India. *J. Mammal.*, 73 (3): 527-534.
- GARCÍA-GONZÁLEZ, R. (1985). Preliminary data on Pyrenean chamois populations in Central Pyrenees. *Munibe*, 37: 5-15. (In spanish).
- GARCÍA-GONZÁLEZ, R.; HERRERO, J. & HIDALGO, R. (1987). Estimation of several population and distributional parameters of Pyrenean chamois in Central Pyrenees. *Pirineos*, 125: 53-63. (In spanish).
- GARCÍA-GONZÁLEZ, R. & HIDALGO, R. (1989). Census and summer-autumn distribution of Pyrenean chamois in Los Valles Hunting Reservation. In: *Symposium Chamois*, Ljubljana (Slovenia), 1988: 225-241. CIC, Paris, France.
- GARIN, I. & HERRERO, J. (1997). Distribution, abundance and demographic parametrs of Pyrenean chamois in Navarre, Western Pyrenees. *Mammalia*, 61 (1). (In press).
- GEIST, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, 14: 205-220.

- GERARD, J. F.; LE PENDU, Y.; MAUBLANC, M. L.; VINCENT, J. P.; POULLE, M. L. & CIBIEN, C. (1995). Large group formation in European roe deer: an adaptive feature? *Rev. Ecol. (Terre Vie)*, 50: 391-01.
- GERARD, J. F. & RICHARD-HANSEN, C. (1992). Social affinities as the basis of the social organization of a Pyrenean chamois (*Rupicapra pyrenaica*) population in an open mountain range. *Behavioural Processes*, 28: 111-122.
- GONZALEZ, G. & BERDUCOU, C. (1985). Les groupes sociaux d'isards et de mouflons, au massif du Carlit (Pyrénées orientales). *Gibier Faune Sauvage*, 4: 85 -102.
- HERRERO, J.; GARIN, I.; GARCÍA-SERRANO, A. & GARCÍA-GONZÁLEZ, R. (1996). Habitat use in a forest Pyrenean chamois (*Rupicapra pyrenaica*) population. *Forest Ecology and Management*, 88: 25-29.
- HIDALGO, R.; CANUT, J.; HERRERO, J. & GARCÍA-GONZÁLEZ, R. (1995). Biology, ecology and management of Pyrenean chamois in the Spanish Pyrenees. *Quercus*, 109: 31-36. (In Spanish with english abstract).
- LEVET, M., & PÉPIN, D. (1994). Sociabilité et domaine vital d'isards (*Rupicapra pyrenaica*) males au printemps à Orlu (Ariège). *Gibier Faune Sauvage, Game Wildl.*, 11: 51-64.
- LOVARI, S. & COSENTINO, R. (1986). Seasonal habitat selection and group size of the Abruzzo chamois (*Rupicapra rupicapra ornata*). *Bollettino di Zoologia*, 53: 73-78.
- MAUBLANC, M.; BIDEAU, E. & VINCENT, J. (1987). Flexibilité de l'organisation sociale du chevreuil en fonction des caractéristiques de l'environnement. *Rev. Ecol. (Terre Vie)*, 42: 109-133.
- NASCETTI, G.; LOVARI, S.; LANFRANCHI, P.; BERDUCOU, C.; MATTIUCCHI, S.; ROSSI, L. & BULLINI, L. (1985). Revision of *Rupicapra* Genus III. Electrophoretic studies demonstrating species distinction of chamois populations of the Alps from those of the Apennines and Pyrenees. In LOVARI, S. (Ed.). *The Biology and Management of Mountain Ungulates*: 56-62. Croom Helm, London.
- NIEVERGELT, B. (1974). A comparison of Rutting Behaviour and Grouping in the Ethiopian and Alpine ibex. In GEIST, V. & WALTHER, F. (Eds.). *The Behaviour of Ungulates and its Relation to Management*: 324-340. IUCN.
- PÉPIN, D. & LAMERENX, F. (1995). Environnement socio-spatial d'une femelle d'isard (*Rupicapra pyrenaica*) avant et après mise bas. *Gibier Faune Sauvage, Game Wildl.*, 12: 271-288.
- PÉREZ-BARBERÍA, J. & NORES, C. (1994). Seasonal variation in group size of Cantabrian chamois in relation to escape terrain and food. *Acta Theriologica*, 39 (3): 295-305.
- PUTMAN, R. J. (1986). *Grazing in temperate ecosystems: large herbivores and the Ecology of the New Forest*. Croom Helm, London, United Kingdom.

- RICHARD-HANSEN, C. & CAMPAN, R. (1992). Social environment of Isard kids, *Rupicapra pyrenaica p.*, during their ontogeny. *Z. Säugetierkunde*, 57: 351-363.
- RICHARD, C. & MENAUT, P. (1989). Seasonal changes in group size and association patterns in a dense population of Isard (*Rupicapra pyrenaica*). *Abstracts of the World Conference on Mountain Ungulates*, Camerino, Italy.
- RICHARD-HANSEN, C. (1992). Associations between individually marked Isards (*Rupicapra pyrenaica pyrenaica*): seasonal and inter-annual variations. In SPITZ, F.; JANEAU, G.; GONZÁLEZ, G.; & AULAGNIER, S. (Eds.) *Ongulés/Ungulates*, 91: 299-304. SFEPM-IRGM, Toulouse.
- RICHARD-HANSEN, C.; GONZÁLEZ, G. & GERARD, J. (1992). Structure sociale de l'isard (*Rupicapra pyrenaica*) dans trois sites pyrénéens. *Gibier Faune Sauvage*, 9: 137-150.
- SCHALLER, G. B. (Ed.) (1977). Mountain Monarchs. Wild Sheep and Goats of the Himalaya. *Wildlife Behavior and Ecology Series*. The University of Chicago Press, Chicago and London.
- SHANK, C. C. (1985). Inter- and intra-sexual segregation of chamois (*Rupicapra rupicapra*) by altitude and habitat during summer. *Zeitschrift für Säugetierkunde*, 50: 117-125.